Litter Fall and Nutrient Cycling in the Forest Floor of Birch and Aspen Stands in Interior Alaska

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During a 4-year period the biomass and mass of selected chemical elements were measured in litter fall from young, intermediate, and mature age classes of quaking aspen and paper birch in interior Alaska.

Average annual deposition of biomass and mass of Mg, Fe, and Mn were consistently greater in birch than in aspen stands of similar age. Mass of Ca was consistently greater in aspen stands (range 4.02 to 4.80 g m^{-2}) than in birch stands (3.18 to 3.45 g m^{-2}) regardless of age class. Trends in mass of chemical elements returned to the forest floor in litter fall were generally reflected in the average percentage composition of the organic matter.

Turnover time for forest-floor biomass was about the same for both the 50- and 120-year age classes of birch (16.7 years) and of aspen (12.7 years to 13.0 years). For both species Fe had the maximum turnover time in the forest floor (167 to 280 years), with K (6.9 years to 9.7 years) and Zn (5.5 years to 11.6 years) having minimum times.

Linear correlations between biomass and mass of selected nutrient elements in litter fall provide an efficient means of conducting short- and long-term assessments of differences in nutrient content of litter within and between forest vegetation types.

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Pour une période de 4 ans, on a mesuré la biomasse et la masse de certains éléments chimiques dans la litière annuelle du peuplier faux-tremble et du bouleau à papier de trois classes d'âge: jeune, intermédiaire et mûr, dans la partie intérieure de l'Alaska.

La déposition annuelle de biomasse, et la masse de Mg, Fe, et Mn étaient d'une façon consistante plus élevées chez les peuplements de bouleau que chez ceux du faux-tremble d'âge similaire. La masse de Ca était toujours plus élevée chez les peuplements de faux-tremble (4.02 à 4.80 g m^{-2}) que chez les peuplements de bouleau (3.18 à 3.45 g m^{-2}), quel que soit l'âge. L'importance de la masse d'éléments chimiques retournés au sol par la litière se traduisait généralement dans la composition chimique de la couverture d'humus.

Le temps de renouvellement pour la biomasse de la couverture d'humus était sensiblement la même pour les classes d'âge de 50 et 120 ans chez le bouleau (16.7 ans) et le faux-tremble (12.7 à 13.0 ans). Chez les deux espèces, Fe présentait le temps de renouvellement maximum dans la couverture d'humus (167 à 280 ans), alors que les temps minimums se manifestaient chez K (6.9 à 9.7 ans) et Zn (5.5 à 11.6 ans).

Les corrélations linéaires entre la biomasse et la masse d'élements nutritifs particuliers de la litière offre un moyen permettant des évaluations à court et à long terme des différences dans la teneur en éléments nutritifs de la litière, à l'intérieur et entre les types de végétation.

[Traduit par le journal]

Introduction

In a previous paper (Van Cleve and Noonan 1971) we described selected physical and chemical properties of the forest floor in paper birch (*Betula papyrifera* Marsh.) and quaking aspen (*Populus tremuloides* Michx.) stands ranging from 10 to 120 years in age. Generally, over this range of ages, aspen forests have greater mass of organic matter and percentage of ash in the forest floor. On the average, about 4200 g m^{-2} are found in aspen forest floor compared with 4000 g m^{-2} organic

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TABLE 1. Stand parameters for birch and aspen stands of selected ages (standard error of mean in parentheses)

Species	Age, years	Basal area, $m^2\ ha^{-1}$	Stem ha^{-1}
Aspen	10	8.1 (0.5)	23 875 (3875)
Aspen	50	43.1 (4.9)	4402 (730)
Aspen	120	52.2 (11.0)	1368 (264)
Birch	25	28.4 (1.4)	14 451 (1378)
Birch	50	26.5 (4.1)	3390 (313)
Birch	120	31.3 (5.1)	417 (60)

matter in birch forest floors, with the floors containing 21% and 16% ash respectively. Higher pH and lower exchangeable hydrogen reflect a more favorable base status in aspen forest floors than in birch floors.

The forest floor is a key compartment in the ecosystem. The close proximity of root systems to the surface organic matter of the soil emphasizes the importance of this material as a source of nutrients for trees. In the cold soils characteristic of subarctic Alaska, forest types developing on well drained, permafrost-free soil have root systems which may penetrate to a depth of 40 to 50 cm; forest types developing on poorly drained, permafrost-dominated soil have root systems which may penetrate to only about 30 cm. In both cases much of the finer portion of tree root systems appears to be concentrated at depths shallower than 30 cm, in the humus (H) layers of the forest floor and in the A horizon of the soil profile. This is the case in the stands considered in the present study.

In this paper we summarize litter-fall biomass and nutrient content and forest-floor biomass and nutrient turnover of selected birch and aspen stands that were included in the previous study. The principal objective of the study was to compare selected aspects of nutrient cycling between vegetation types of the same age.

Study Areas

With the exception of the 10-year-old aspen stand, study areas were located in upland sites extending about 40 km northeast of Fairbanks, Alaska, along the upper Chena River Valley. The 10-year-old aspen stand was located on an old terrace of the upper Chena River. Soil at this site is a deep, well drained sandy loam. For the remaining areas, bedrock is Birch Creek schist, a Precambrian formation of folded and strongly pointed quartz–mica and quartzite schist. Soils of the upland sites have developed from micaceous loess which was deposited during the last glacial epoch. The depth of the deposits varies from 30 cm or less in high positions to about 61 m on low hills bordering the Tanana River (Rieger *et al.* 1963). The dominant texture of soil in these areas is silt or silt loam. Rock content of the soil in all sample areas is negligible. The mean annual temperature and precipitation for the general area are −3.4 °C and 28.7 cm, respectively (U.S. Weather Bureau 1966).

All of the sample stands examined in this study had developed after fire. Charred stumps and charcoal deposits in the A horizon of mineral soil profiles were repeatedly encountered in the respective study sites. The young (10 years old) aspen stand was included in the study because of its recent fire history and the lack of another forest of this age on an upland location within the general area. The relationship between fire and forest succession in interior Alaska is discussed in detail by Lutz (1956).

Even-aged stands of birch and aspen of various ages are numerous in the study area. The uniform soil simplifies selection of sample areas in which productive capacity is similar. In selecting sample stands, we attempted to maintain uniform site conditions (slope, aspect, position on slope). Three stands of birch, from 25 to 120 years in age, and three of aspen, from 10 to 120 years in age, were selected for intensive sampling. Basal area for these stands is summarized in Table 1. During midsummer to late summer 1967, before leaf fall, samples of the forest floor were collected in each stand. Methods used in this

part of the study are summarized in a previous paper (Van Cleve and Noonan 1971). Stand age was determined from increment cores at breast height from several of the larger trees in each sample area.

Metre-square litter screens, 76 per hectare, covering about 0.8% of the sample area (Newbould 1967; Heller 1971), were placed randomly in each of the six sample stands before leaf fall in August 1967. Subsequently, litter fall was collected weekly during periods of heavy deposition, as soon as possible after snowmelt in the spring, and before leaf fall in early August. This sampling regime was followed through the fall of 1970.

Laboratory Methods

All organic matter samples were dried at 65 °C to a constant weight (normally 48 h) and weighed. Litter tray samples were separated into three categories; leaf, branch (all material 2 mm in basal diameter and larger), and seed and miscellaneous. The latter included rabbit pellets, small-particle-size leaf material, birch cone bracts, etc. The separates were ground to pass a 40-mesh Wiley mill sieve. Organic matter content was determined using a dry combustion method (Jackson 1958), and nitrogen was determined by the micro-Kjeldahl procedure (Jackson 1958). Total phosphorus was determined on a perchloric acid digest using the ammonium molybdate technique with amino-naptholsulfonic-acid reducing agent (Jackson 1958). Total Ca, Mg, K, Mn, Zn, and Fe were determined in aliquots of the perchloric acid digest using an atomic absorption spectrophotometer. Strontium chloride was added to the Ca and Mg aliquots to suppress anion interference. All analyses were carried out in duplicate.

Calculations

Data for forest-floor and litter-fall biomass and mass of selected chemical elements are expressed as grams per square metre oven-dried weight. Biomass turnover is summarized on an ash-free basis. Fractional annual turnover values were calculated using the approach of Jenny *et al.* (1949). A steady state was assumed for the forest floor in both 50- and 120-year-old aspen and birch stands. Biomass and nutrient status of the first floor were measured in the late summer of 1967. Therefore, litter-fall biomass and nutrient data from 1967 were used in these calculations.

Standard errors of the means over 4 years were calculated to assess between-year variation for all biomass and nutrient data. Errors for yearly data were also calculated and generally showed the same degree of variation for various litter categories as encountered across the 4-year period. Error calculations were carried out within species and age classes.

For each vegetation type, age class, and category of litter and nutrient, the data for replicate trays from each sampling time for all years were plotted as a function of biomass (dry-weight basis) of the respective litter category. In nearly all cases linear relationships were found. To predict the mass of a selected nutrient in a given mass of bulk litter fall for the respective vegetation types and age classes, summations were separately calculated of biomass and mass of nutrients for all litter categories for the material from each tray for each sampling time during the 4-year period. Each summation was considered a sample point for the subsequent analyses. Linear regression analysis was performed on the summations for each year and across all 4 years to establish the mathematical relationship between mass of nutrient and biomass of any given sample of litter fall. Slopes of regression lines calculated for the total 4-year period were compared between vegetation types within similar age classes using an "F" test to establish the significance of differences. The slopes of lines when multiplied by 100 give an estimate of the average percentage composition of the litter fall in each vegetation type during the 4-year study period. Regression lines were not forced through the origin.

The significance of differences in 4-year average biomass and mass of nutrients in the respective litter-fall categories and total litter between vegetation types, within similar age classes, and for total litter only within vegetation types across age classes were tested using a "t" test. Fractional annual turnover values for biomass and selected nutrients were tested between age classes for significance of differences within vegetation types and within age classes across vegetation types using a "t" test. Only the 50- and 120-year-old age classes in each vegetation type were included in the latter tests.

Results

Stand Characteristics and Biomass and Nutrient Content of the Forest Floor

Basal area in birch stands was slightly greater at 25 years than at 50 years, and maxi-

mum basal area (31.3 m^2 ha^{-1}, Table 1) was attained at 120 years. Basal area in the aspen forests increased from 8.1 to 52.5 m^2 ha^{-1} from 10 years to 120 years. Basal area was markedly greater in aspen than in birch at 50 and 120 years. Tree densities were highest in the younger age class forests and decreased regularly to about 417 stems ha^{-1} at 120 years in birch. Lower stem densities were encountered for all age classes in birch than in aspen forests.

For the range of age classes in the present study, biomass and mass of nutrients in the forest floor generally showed an increasing trend with age (Table 2). Mass of Ca, P, and Zn was consistently higher in aspen forest floors at 50 and 120 years than in birch forest floors at the same age. Greater mass of N, Mg, and Fe was found in birch forest floor at 50 and 120 years. Manganese was higher in aspen forest floors at 50 years and in birch at 120 years.

Biomass and Mass of Nutrients in Litter Fall

Between-year variation in biomass and mass of nutrients was generally a smaller proportion of the leaf litter category than of the branch or seed and miscellaneous categories, regardless of vegetation type or age class (Table 3). With regard to aspen, between-year variation in total biomass of litter fall varied from 5% (50-year age class, Fig. 1) to 16% (120-year age class). Between-year variation in total litter-fall nutrient varied from 8% to 22% of the 4-year average depending on the nutrient considered.

In aspen litter fall, significant increases in average annual deposition of total biomass and mass of nutrients generally occurred with age up to 50 years. No significant differences (for biomass, N, Ca, Mg, Fe, Mn, Zn) or significant decreases (for P, K) were encountered between 50 and 120 years depending on the variable considered (Table 3). Trends in total litter-fall biomass and mass of nutrients generally reflected the trends in leaf litter fall, the dominant component in litter fall during the study period. Branch and seed and miscellaneous categories generally showed increasing biomass and mass of nutrients up to 120 years. Significance of differences in these categories was not tested within species and litter categories across age classes.

With regard to birch, between-year variation in total biomass of litter fall varied from 8% (25-year age class) to 10% (50- and 120-year age classes, Fig. 2, Table 3). Between-year variation in birch total litter-fall nutrient content varied from 8% to 18% depending on the nutrient considered. Significant increases in average 4-year deposition of Mn and N were encountered at 50 and 120 years respectively while the average deposition of P and K was greatest at 25 years (Table 3). Trends in total biomass and mass of nutrients generally reflected the trends in leaf litter fall, the dominant component in litter during the study period. Greatest biomass of branches and seeds plus miscellaneous litter was encountered at 25 years. Mass of nutrients in both these categories combined were the same at 25 and 50 years and generally the same or slightly larger at 120 years, as in the case of N and Ca (Table 3).

Comparisons within the 50-year age classes between vegetation types showed average biomass (both ash-free and ovendry-weight basis), and P, Fe, and Mn deposition in total litter fall to be significantly greater in birch than in aspen (Table 3, Figs. 1 and 2). Greater amounts of N, K, and Ca were in average aspen litter-fall totals, although only Ca showed a significant difference. Similar average amounts of P and Zn were deposited in both vegetation types within the 50-year age class.

Within the 120-year age class greater biomass (ash-free and dry-weight basis) and significantly more N, P, K, Mg, Mn, and Zn were returned to forest floor in total litter fall in birch than in aspen (Table 3). Similar amounts of Fe were deposited in total litter fall in both vegetation types, but significantly more Ca was returned to the forest floor in the aspen than in birch.

Because of greater stand age and basal area (Table 1) significantly larger amounts of biomass and mass of N, P, K, Mg, Fe, Mn, and Zn were deposited in litter fall of the 25-year-old birch forest than in the 10-year-old aspen forest (Table 3). About the same amounts of Ca were deposited in both forests.

Relationship between Biomass and Mass of Nutrients in Litter Fall

Functional relationships between dry-weight biomass and mass of nutrient elements in the

TABLE 2. Average mass and nutrient content of forest floor in different age classes of birch and aspen forests (g m^{-2}, standard error of mean in parentheses)

Species	Age, years	Biomass (ash free)	N	P	K	Ca	Mg	Fe	Mn	Zn
Aspen	10	508.2 (46.8)	8.9 (1.2)	0.7 (0.1)	0.8 (0.1)	11.2 (1.3)	0.8 (0.1)	0.9 (0.1)	0.1 (0.0)	0.1 (0.0)
Aspen	50	3828.0 (254.3)	76.1 (8.7)	8.1 (0.5)	8.8 (0.7)	68.0 (6.4)	10.8 (1.5)	27.9 (6.5)	9.4 (2.0)	0.3 (0.1)
Aspen	120	5922.6 (1381.2)	107.5 (14.2)	8.6 (1.4)	13.0 (2.0)	78.6 (22.2)	16.7 (1.4)	27.6 (3.8)	7.8 (1.6)	0.6 (0.1)
Birch	25	2107.8 (199.2)	40.5 (1.6)	3.5 (0.1)	4.1 (0.2)	32.4 (2.1)	6.0 (0.5)	7.2 (0.2)	5.3 (0.9)	0.3 (0.1)
Birch	50	4390.8 (745.2)	84.6 (14.2)	7.9 (1.4)	9.9 (2.0)	48.9 (8.3)	13.9 (2.5)	43.0 (19.2)	4.4 (0.3)	0.2 (0.1)
Birch	120	4919.5 (874.9)	104.7 (15.8)	6.9 (0.9)	11.2 (2.0)	67.9 (6.8)	12.0 (1.5)	27.4 (5.1)	11.0 (3.0)	0.4 (0.1)

TABLE 3. Annual averages (over 4 years) for biomass and mass of selected nutrients (g m^{-2} y^{-1}) in litter fall*

Species	Age	Category	Biomass †	N	P	K	Ca	Mg	Fe	Mn	Zn
Aspen	10	Leaves	109.99a (6.51)	0.90a (0.13)	0.20a (0.02)	0.52a (0.06)	2.39 (0.22)	0.37a (0.03)	0.06a (0.01)	0.02a (0.00)	0.010a (0.001)
		Branches	20.45b (9.18)	0.18 (0.10)	0.01 (0.01)	0.02 (0.01)	0.43 (0.19)	0.01 (0.01)	0.01 (0.01)	0.00	0.002b (0.001)
		Seeds and misc.	0.71 (0.64)	0.01b (0.01)	0.00	0.00	0.02 (0.02)	0.00	0.00	0.00	0.000c
		Σ	131.15dfg (13.73)	1.09fhi (0.15)	0.21df (0.02)	0.54df (0.06)	2.84ef (0.38)	0.38dgh (0.04)	0.07eg (0.01)	0.02dgh (0.00)	0.012fhi (0.001)
	50	Leaves	177.80c (12.76)	1.97c (0.32)	0.44 (0.04)	0.88b (0.12)	4.26a (0.47)	0.63 (0.07)	0.07b (0.01)	0.07b (0.01)	0.018d (0.002)
		Branches	31.91 (11.52)	0.11 (0.03)	0.02 (0.00)	0.06 (0.01)	0.39 (0.11)	0.03 (0.01)	0.01 (0.01)	0.00	0.003 (0.001)
		Seeds and misc.	8.94 (2.21)	0.15 (0.04)	0.02 (0.00)	0.02 (0.01)	0.15 (0.04)	0.02 (0.01)	0.01 (0.00)	0.01 (0.00)	0.001 (0.000)
		Σ	218.65ef (11.69)	2.23h (0.37)	0.48fgh (0.04)	0.96fg (0.11)	4.80ce (0.38)	0.68eg (0.06)	0.09fg (0.01)	0.08eg (0.01)	0.022h (0.002)
	120	Leaves	162.31 (25.20)	1.35d (0.23)	0.27b (0.04)	0.47c (0.07)	2.81 (0.47)	0.53c (0.04)	0.06c (0.01)	0.04c (0.01)	0.019e (0.003)
		Branches	44.07 (23.24)	0.23 (0.12)	0.03 (0.01)	0.11 (0.05)	0.97b (0.51)	0.06 (0.03)	0.02 (0.01)	0.01 (0.01)	0.004 (0.002)
		Seeds and misc.	16.00 (3.60)	0.36e (0.10)	0.04c (0.01)	0.04 (0.01)	0.24 (0.06)	0.03 (0.01)	0.01d (0.00)	0.01 (0.00)	0.002 (0.000)
		Σ	222.17g (34.95)	1.94gi (0.35)	0.34egh (0.05)	0.62eg (0.08)	4.02df (0.76)	0.62fh (0.09)	0.09 (0.02)	0.06fh (0.01)	0.025gi (0.004)
Birch	25	Leaves	188.29a (20.00)	1.38a (0.15)	0.52a (0.06)	1.26a (0.15)	2.42 (0.26)	0.81a (0.09)	0.08a (0.01)	0.23a (0.03)	0.024a (0.003)
		Branches	61.48b (21.00)	0.23 (0.08)	0.02 (0.01)	0.07 (0.02)	0.34 (0.12)	0.04 (0.01)	0.01 (0.00)	0.01 (0.00)	0.006b (0.002)
		Seeds and misc.	13.79 (2.50)	0.20b (0.04)	0.03 (0.01)	0.05 (0.01)	0.15 (0.03)	0.03 (0.01)	0.01 (0.00)	0.01 (0.00)	0.003c (0.001)
		Σ	263.56d (20.83)	1.81fk (0.15)	0.57di (0.05)	1.38dhi (0.14)	2.91 (0.25)	0.88d (0.08)	0.10eh (0.01)	0.25dij (0.03)	0.033fj (0.002)
	50	Leaves	208.67c (7.30)	1.47c (0.08)	0.46 (0.02)	0.76b (0.10)	3.03a (0.23)	0.85b (0.03)	0.09b (0.01)	0.28b (0.01)	0.015d (0.002)
		Branches	42.11 (21.40)	0.23 (0.05)	0.02 (0.01)	0.07 (0.02)	0.34 (0.11)	0.04 (0.02)	0.01 (0.01)	0.01 (0.01)	0.006 (0.001)
		Seeds and misc.	13.79 (2.50)	0.20 (0.04)	0.03 (0.00)	0.05 (0.01)	0.15 (0.03)	0.03 (0.01)	0.01 (0.00)	0.01 (0.00)	0.003 (0.001)
		Σ	264.57e (26.98)	1.80j (0.14)	0.50i (0.02)	0.83h (0.06)	3.45c (0.31)	0.92ei (0.11)	0.12fh (0.02)	0.30ei (0.02)	0.020jk (0.003)
	120	Leaves	178.76 (16.90)	1.73d (0.22)	0.42b (0.04)	0.90c (0.05)	2.64 (0.32)	0.75c (0.06)	0.08c (0.01)	0.28c (0.02)	0.023e (0.003)
		Branches	30.85 (11.80)	0.17 (0.06)	0.02 (0.01)	0.05 (0.02)	0.24b (0.09)	0.03 (0.01)	0.01 (0.00)	0.01 (0.00)	0.004 (0.001)
		Seeds and misc.	35.13 (4.60)	0.66e (0.10)	0.07c (0.01)	0.10 (0.01)	0.30 (0.04)	0.07 (0.01)	0.02d (0.00)	0.03 (0.00)	0.004 (0.001)
		Σ	244.74 (25.01)	2.56gjk (0.29)	0.51e (0.05)	1.05ei (0.10)	3.18d (0.39)	0.85fi (0.07)	0.11 (0.02)	0.32fj (0.03)	0.031gk (0.004)

*Values associated with same letters are significantly different at 5% level, "*t*" test; standard error of mean in parentheses is index of between year variation in mean values.
†Dry-weight basis.

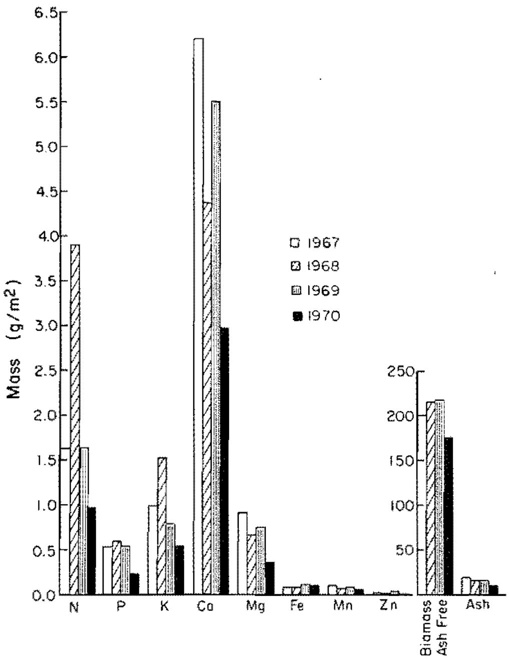

FIG. 1. Average yearly mass of organic matter and selected nutrients in litter fall of 50-year-old aspen stand.

total litter fall generally showed higher degrees of correlation for macronutrient than for micronutrient elements (Table 4). Significant year-to-year variation in slopes of regression lines (percentage nutrient content on dry-weight basis) was encountered within vegetation types for most nutrients. However, for birch, no between-year differences in percentage N or Fe were encountered in the 50- or 120-year age classes. For 10-year-old aspen no between-year difference was found for litter percentage N, P, K, Ca, Mg, or Fe. The 50-year age class aspen showed no significant yearly variation for percentage Fe and percentage Mn while the 120-year age class showed no between-year differences for percentage Mn and Zn.

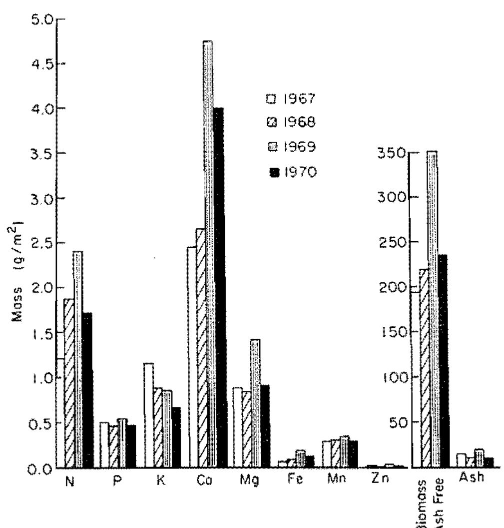

FIG. 2. Average yearly mass of organic matter and selected nutrients in litter fall of 50-year-old birch stand.

With regard to the 50-year age class, aspen total litter showed significantly greater average concentration of N, Ca, and Zn than birch while birch showed significantly greater concentrations of Mg and Mn. No differences between vegetation types were encountered for P, K, and Fe. In contrast with the concentrations, average mass of N and Zn showed no differences between vegetation types (Table 3).

With the exception of N (no significant difference in concentration between aspen and birch) the percentage nutrient content of aspen and birch litter fall at 120 years showed the same relationships between species found for mass of nutrients (Table 3). Significantly greater concentrations of P, K, Mg, Mn, and Zn were encountered in birch than in aspen, while aspen litter fall showed the highest Ca content (Table 4). Between vegetation type differences for N and P were not significant.

For the youngest age classes, N, Ca, and Mn showed highest concentrations in aspen litter fall while P, K, and Zn showed highest concentration in birch litter fall. Significant differences between vegetation types did not exist for Mg and Fe.

Discussion and Conclusions

Biomass and Nutrient Content of Litter Fall

Amounts of organic matter and nutrients returned to the forest floor may reflect the density and basal area of the respective sample forest stands (Bray and Gorham 1964). In the present study, with the exception of the 25- to 50-year period in birch, for both species stem density decreases and basal area increases with increasing stand age (Table 1). With regard to aspen, increasing basal area (decreasing stem density) appears to be related to increasing total litter-fall biomass (Tables 1

TABLE 4. Comparison of nutrient content (y, g m^{-2} y^{-1}) of litter fall with biomass of litter fall (x, g m^{-2} y^{-1}) for 50-year-old age class of birch and aspen stands

Element	Species	Equation	R^2	F, difference between slopes[a]	F, slope = 0	$Sy{\cdot}x$[b]
N	Birch	$y = 0.005958x + 0.053252$	0.89	7.2 (1, 108)**	436.9	0.093
	Aspen	$y = 0.008425x + 0.055120$	0.61		81.8	0.271
K	Birch	$y = 0.003738x - 0.002947$	0.73	NS (1, 108)	151.0	0.099
	Aspen	$y = 0.003896x + 0.013877$	0.84		269.9	0.069
P	Birch	$y = 0.002304x - 0.011960$	0.91	1.84 (1, 108)	551.1	0.032
	Aspen	$y = 0.002125x - 0.010729$	0.90		449.9	0.034
Ca	Birch	$y = 0.015285x - 0.070532$	0.84	90.79 (1. 108)**	300.4	0.288
	Aspen	$y = 0.028887x - 0.199573$	0.92		639.7	0.332
Mg	Birch	$y = 0.004457x - 0.028233$	0.92	6.28 (1, 108)*	616.7	0.059
	Aspen	$y = 0.003871x - 0.019715$	0.94		765.2	0.041
Fe	Birch	$y = 0.000335x + 0.005603$	0.65	NS (1, 108)	104.3	0.0107
	Aspen	$y = 0.000324x + 0.003276$	0.48		48.6	0.0135
Mn	Birch	$y = 0.001457x - 0.010246$	0.92	274.9 (1,108)**	683.0	0.0182
	Aspen	$y = 0.000411x - 0.002305$	0.89		424.4	0.0058
Zn	Birch	$y = 0.000068x + 0.000412$	0.48	4.79 (1, 108)*	51.8	0.0031
	Aspen	$y = 0.000095x + 0.000531$	0.78		183.1	0.0020

[a]**, difference between slopes between comparable-aged birch and aspen stands significant at 1% level of probability; values in parentheses are degrees of freedom; *, difference between slopes between comparable-aged birch and aspen stands significant at 5% level of probability; values in parentheses are degrees of freedom; NS, not significant.
[b]$Sy{\cdot}x$ = standard error of estimate.

and 3). With regard to birch, litter-fall biomass is highest in high-stem-density younger age classes (25- and 50-year-old birch) and lowest in the low-stem-density 120-year-old age class. Obviously, three age classes in each vegetation type is a restricted sample upon which to draw any conclusions concerning relationships between litter fall, stocking, and basal area.

During the 4-year study period, leaf fall in the 10-, 50, and 120-year-old aspen forests comprised 84%, 81%, and 73%, respectively, of average total litter-fall biomass, and branch fall comprised 16%, 15%, and 20%, respectively (Table 3). During the same time, leaf fall in 25-, 50-, and 120-year-old birch forests comprised 71%, 79%, and 73%, and branch fall comprised 23%, 16%, and 13%, respectively, of average total litter-fall biomass. Distribution of litter production between these categories reflects stand development. Crown canopy in the 10-year-old aspen forest has not completely developed and individual trees have a more open-grown form, with little shading of lower branches with their eventual death and natural pruning occurring. During later stages of forest development (120 years), death of branches from lower portions of tree crowns in combination with greater mass of individual branches probably results in the greater contribution of branch litter to the forest floor.

A dense canopy exists in the 25-year-old birch forest. Extensive natural pruning and stem death is evident at this stage in stand development. Subsequently, at 50 and 120 years the stand is more open and branch material comprises a smaller portion of the litter fall. Both vegetation types probably pass through similar stages in component distribution in litter fall, but lack of appropriate age classes did not allow this to be tested. Alternatively, the generally increasing contribution of branch material with age in aspen litter fall compared with a general decrease with age in birch litter fall may reflect differences in allocation of production between the two species. At the time of study, extensive death of trees or deposition of bole material on the forest floor was not occurring in the oldest age classes in either forest type. Differences in site quality must also be considered, although

measurement showed site index to be about the same within birch and aspen vegetation types.

Within-season variation in litter-fall nutrient content may be attributed to a number of factors. Translocation of nutrients from leaves as time of senescence approaches, extent of leaching of soluble organic and inorganic nutrients out of leaf material, extent of decomposition of leaves before fall, and proportion of leaf to branch and other litter components may affect concentration and total content of the respective elements in any one collection of litter fall.

Translocation of elements from leaf tissue before abscission may have considerable effect on their percentage concentration in the tissue (Gosz *et al.* 1972). In the present study late-summer (early August) senescent leaf material generally showed higher concentrations of more mobile nutrients such as N and lower concentrations of less mobile nutrients such as Ca than later (September) during periods of heaviest leaf fall. During the latter period a shift in nutrient concentration occurred with N concentration decreasing and Ca concentration increasing in senescent leaf material, presumably in part a result of translocation of mobile nutrients out of the leaves and accumulation of less mobile elements before abscission. Total percentage ash generally followed the seasonal trends noted for Ca. These trends, which generally appeared regardless of age class or vegetation type, were similar to those noted by Gosz *et al.* (1972).

In addition to translocation, leaching of soluble organic and inorganic constituents from leaf material may have marked influence on nutrient content of senescing foliage (Tukey 1970). Mobile elements such as N and K and soluble low-molecular-weight organic constituents may be removed from leaves by various forms of precipitation (dew, fog drip, rainfall), while less mobile elements such as Ca would not be leached to the same degree and could accumulate. Microbial decomposition of senescing leaf tissue before fall would result in loss of biomass through respiration and, in conjunction with leaching, may promote increases in concentration of less mobile elements in the organic matter.

Proportions of branch to leaf tissue greatly influence the total nutrient content of litter fall. Regardless of vegetation type, age class, year of sampling, or nutrient, leaf material generally had a higher percentage nutrient content than branch material. For spring and late-summer collections branch material comprised from 30% to over 50% of litter-fall biomass while 90% to 100% of the material collected during periods of heavy litter fall consisted of leaf tissue. Seasonal distribution of nutrient flux to the forest floor reflected the varying composition of the litter with regard to the major categories. In addition to the above factors between-year variation in biomass and mass of nutrients in litter fall undoubtedly reflects the controlling effects of temperature and precipitation in relation to tree growth and nutrient uptake.

An example of the linear relationship typical for all nutrients considered between total litter-fall biomass and mass of nutrient is shown in Fig. 3. Relatively small biomass and mass of nutrients in litter fall, occurring during the winter months, or during early spring before snowmelt and collected after snowmelt, are seen at the lower end of the regression lines. Larger deposition of litter and associated nutrients encountered during the fall are scattered along the entire length of the regression lines. Smaller fall samples represent those collections made just before leaf fall and after major deposition of litter before winter snowfall.

Correlation between biomass and mass of nutrients in total litter fall (or its components) may be of value from several standpoints. If a sufficient period of time is allowed for calibration of individual sites during which intensive measurement of biomass and nutrient content of detritus is carried out, the regression relations between these parameters can be established. Subsequent estimates of nutrient flux in litter fall could be obtained at considerably reduced expense by measurements of biomass followed by calculation of nutrient mass using the appropriate equations. However, comparisons of ecosystem processes across small or large geographic ranges must be considered in light of differences in state factors (Jenny 1941) and differences in sam-

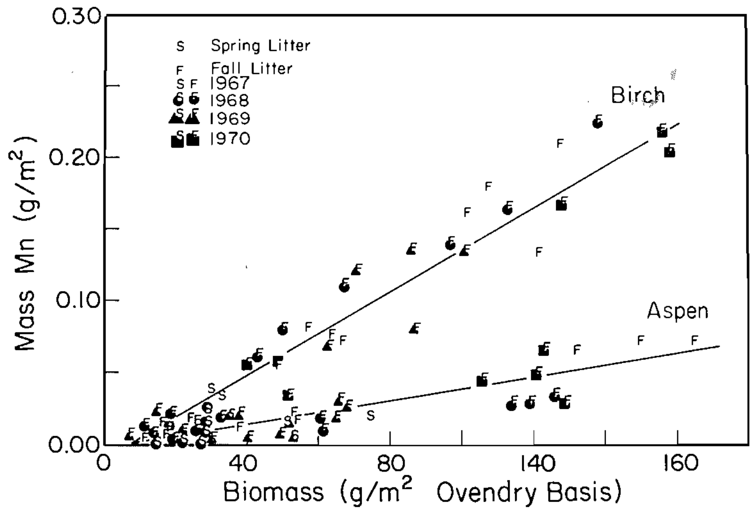

FIG. 3. Relationship between mass of Mn and litter-fall biomass (dry-weight basis) for seasonal samples collected in 50-year-old stands of birch and aspen.

pling and analytical techniques between investigators. The correlations considered in this study are undoubtedly highly specific for the states of the respective ecosystems considered in the study.

Comparison of Litter-fall Production between Different Geographic Regions

Birch and aspen stands in the present study showed 4-year average annual total litter production ranging from 2.4 to 2.6 metric tons ha^{-1} and 1.3 to 2.2 metric tons ha^{-1}, respectively (dry-weight basis). Finnish birch forests had annual production of 1.9, 1.5, and 1.8 metric tons ha^{-1} y^{-1}, respectively, for 52-, 86-, and 91-year-old stands (Bray and Gorham 1964). *Betula verrucosa* stands in Voronezh province, U.S.S.R., produced 4.1 and 2.9 metric tons ha^{-1} y^{-1} at 25 and 62 years old, respectively (Rodin and Bazilevich 1967). Four and 8% of these totals, respectively, were twigs and bark. Ten- and 50-year-old *Populus tremula* stands in the same geographic region produced 3.9 and 4.9 metric tons ha^{-1} y^{-1}, respectively, of litter fall. Three and 8% of these totals were twigs and bark. Proportions of twig and bark material in litter fall were generally less than half that encountered in birch and aspen litter fall in the present study. Litter production for the Alaska forests appears to most closely approximate litter production in the Finnish forest.

Estimates of litter production have been obtained for alder and alder–willow forests in Alaska. Hurd (1971) estimated annual litter production for mixed *Alnus–Salix* stands dominated by *Alnus crispa* near Juneau, Alaska, to be about 2.3 to 3.0 metric tons ha^{-1} y^{-1}. Van Cleve *et al.* (1971) determined foliar weights in 5-, 15-, and 20-year-old stands of *Alnus incana* of 1.8, 1.6, and 2.1 metric tons ha^{-1}, respectively. All of these estimates are in the range of values determined for total average litter fall in the aspen and birch forests (Table 3).

Total litter production average for all age classes of birch (2.6 metric tons ha^{-1} y^{-1}) and aspen (1.9 metric tons ha^{-1} y^{-1}) is below the average of 3.2 metric tons ha^{-1} y^{-1} calculated by Bray and Gorham (1964) for northern-hemisphere deciduous angiosperm forests. In relationship to litter production by forests in other major climatic zones of the world, these averages are about midway between average litter production encountered in cool temperate zone (3.5 metric tons ha^{-1} y^{-1}) and arctic–alpine zone (1.0 metric tons ha^{-1} y^{-1}) forests (Bray and Gorham 1964). Average annual litter production for the birch and aspen forests is higher than the average of 1 metric ton ha^{-1} y^{-1} predicted by Bray and Gorham (1964, Fig. 1, p. 128) for forests at 64 °N latitude.

Nitrogen content of litter fall in the 25- and

62-year-old *Betula verrucosa* forests totaled 32.8 kg ha^{-1} y^{-1} and 34.3 kg ha^{-1} y^{-1}, respectively (Rodin and Bazilevich 1967). Mass of nitrogen in litter fall from 10- and 50-year-old *Populus tremula* stands from Voronezh province, U.S.S.R., totaled 41.0 kg ha^{-1} y^{-1} and 46.0 kg ha^{-1} y^{-1}, respectively. In the present study, range for mass of N was 1.8- to 1.3-fold less for 25- to 120-year-old birch and 3.8- and 2.1-fold less for 10- to 120-year-old aspen. Values for P, K, Ca, Mg, Fe, and Mn in litter fall for the 50-year-old *Populus tremula* stand are 5, 81, 102, 10, 1, and 1 kg ha^{-1} y^{-1}, respectively. These values are about the same for P, Fe, and Mn but 8.4-, 2.1-, and 1.5-fold greater respectively, for P, Ca, and Mg in the *P. tremula* compared with the Alaska *P. tremuloides* stands at 50 years.

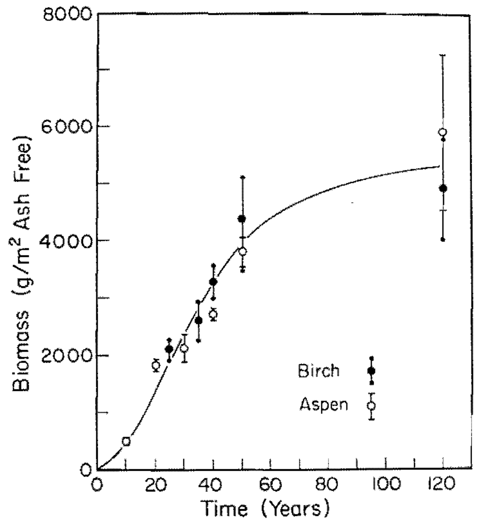

FIG. 4. Relationship between forest-floor biomass and time for birch and aspen forests of various ages.

Biomass and Nutrient Turnover in the Forest Floor

The principal assumption with respect to calculation of forest-floor decomposition constants is the existence of a steady state with regard to gains and losses of biomass and mass of nutrients in this ecosystem compartment. Two lines of evidence indicate that at 120 years birch and aspen forest floors may be approaching or in steady state. Graphical presentation of forest-floor biomass in relationship to time for various age-class birch and aspen forests indicates an asymptotic approach to a relatively constant forest-floor biomass (Fig. 4).

A second line of evidence is related to the longevity of these vegetation types in the Tanana–Yukon uplands. Depending on site quality, after a period of 90 to 100 years, birch and aspen stands begin to disintegrate, probably in large part because of infection by fungi (Gregory and Haack 1966). The 120-year age classes in the present study represent advanced stages in the life history of birch and aspen forests in this geographic region. The possibility for encountering steady-state forest-floor conditions within a vegetation type are undoubtedly best at maximal age of forest development, before disintegration of the forest.

Based upon the forest-floor biomass accumulation relationships (Fig. 4) and age of the oldest stands considered in this study, a steady-state condition was assumed for the forest floor in the oldest birch and aspen stands. Since the 50-year-old birch and aspen stands appear to be near a breaking point in the forest-floor-biomass-accumulation – time relationship the same assumption was applied to these stands.

More rapid annual turnover of Mn (1.9-fold) and Zn (2.0-fold) at 50 years and N (1.3-fold) at 120 years was encountered in birch (Table 5). For birch, relatively large differences between 50 and 120 years for P, K, Ca, and Mg were not significant at the 5% level of probability. Biomass turnover was the same for both age classes.

Most rapid turnover of Mg (11.5%) was noted at 50 years in aspen. For aspen, relatively large differences between 50 and 120 years for other elements (P, K, Ca, Zn) were not significant at the 5% level of probability. Biomass turnover was the same at 50 and 120 years in aspen.

Turnover of N, Ca, and Mg was more rapid in aspen at 50 years than in birch at 50 years (1.7-fold, 1.8-fold, and 1.4-fold, respectively, Table 5) while turnover of Mn and Zn was 5.3-fold and 1.8-fold, respectively, more rapid at 50 years in birch than in aspen. Average biomass turnover for both age classes was about 30% greater for aspen than birch, although differences were not significant.

Ranking of annual turnover values for both age classes of aspen generally shows K, Ca,

TABLE 5. Fractional annual turnover (%, standard error of mean in parentheses) for selected chemical elements in birch and aspen forest floors.* (Annual input in mass of constituents in litter fall per mass of constituents on forest floor × 100.)

Species	Age years	N	P	K	Ca	Mg	Fe	Mn	Zn	Biomass
Birch	50	2.1ab (0.2)	8.2 (1.1)	13.4 (1.6)	7.1a (0.8)	8.3a (1.0)	0.4 (0.1)	8.5ab (1.4)	18.2ab (4.11)	6.0 (0.7)
	120	2.8a (0.3)	9.2 (0.7)	13.9 (1.9)	5.0b (0.1)	9.5 (0.5)	0.4 (0.1)	4.5a (1.6)	9.3a (1.2)	6.0 (1.0)
Aspen	50	3.5b (0.0)	9.3 (0.2)	14.4 (0.5)	12.5a (1.2)	11.5ab (0.4)	0.5 (0.1)	1.6b (0.2)	10.2b (2.0)	7.7 (0.6)
	120	3.3 (0.2)	9.2 (1.0)	10.3 (1.4)	9.9b (2.0)	9.3b (0.8)	0.6 (0.1)	1.8 (0.3)	8.6 (1.0)	7.9 (0.9)

*Values associated with same letter significantly different at 5% level. Calculations based on litter-fall data for the year 1967. Turnover time in years = 1/fractional annual turnover.

TABLE 6. Summary of mobility series for selected nutrient elements in forest floors of different vegetation types

Author	Species and location	Mobility series (based on fractional annual turnover)
Attiwill (1968)	*Eucalyptus obliqua*, Australia	K > Ca > Mg > P
Reiners and Reiners (1970)	*Quercus* forest, Minnesota, U.S.A.	N > P > Mg > Ca
Ulrich *et al.* (1971)	*Fagus* forest (125 years), Germany	Mn > K > Ca > P > N > Mg > Fe
Cole *et al.* (1967)	*Pseudotsuga menziesii*, Western Washington, U.S.A.	K > Ca > N > P
Van Cleve and Noonan (this paper)	*Populus tremuloides* (50 years),	K > Ca > Mg > Zn ≥ P > N > Mn > Fe
	" " (120 years),	K > Ca > Mg ≥ P > Zn > N > Mn > Fe
	Betula papyrifera (50 years),	K = Zn > Mn ≥ Mg ≥ P > Ca > N > Fe
	" " (120 years),	K > Mg ≥ Zn ≥ P > Ca > Mn > N > Fe
	Fairbanks, Alaska, U.S.A.	

and Mg greater than N, Mn, and Fe with Zn and P in intermediate positions. This mobility series is similar to that determined by Attiwill (1968) for *Eucalyptus obliqua* stands in Australia. Ranking of annual turnover values for both age classes of birch show that N and Fe have the slowest turnover rates. No consistency between age classes occurs for the rest of the elements. At 50 years the ranking is $K = Zn > Mn \geqslant Mg \geqslant P > Ca > N > Fe$, and at 120 years the ranking is $K > Mg \geqslant Zn \geqslant P > Ca > Mn > N > Fe$. Considering average nutrient mobilities for both age classes between vegetation types, Ca and Mg are turning over, respectively, 1.8 and 1.2 times more rapidly in aspen while Mn and Zn are turning over, respectively 3.8 and 1.5 times more rapidly in birch.

The range of values for annual biomass turnover in the present study (about 6% to 8%) is slightly less than half that encountered by Attiwill (1968, 16.3%) for *Eucalyptus obliqua* forest floors but similar to the value obtained by Reiners and Reiners (1970, 6.7%) for an oak forest in Minnesota. Biomass turnover values for the Alaskan birch and aspen forest floors are in the range of values reported by Jenny *et al.* (1949) for black oak forests (*Quercus kellogii*) in the Sierra Nevada of California (5.6% to 11.7%).

Fractional annual turnovers calculated for P, Mg, Ca, and K and averaged for birch and aspen stands were about twofold less than values calculated by Attiwill (1968) for the eucalyptus stands. Average turnover values in birch stands for N, P, Ca, and Mg were equal to, 2.4-fold greater, and 1.7-fold and 1.1-fold less, respectively, than values for these elements determined in the Minnesota oak forest (Reiners and Reiners 1970). Averaged turnovers in aspen were equal for Mg and 1.3-fold, 2.6-fold, and 1.1-fold greater for N, P, and Ca, respectively, than values calculated for the Minnesota oak forest.

In general, mobility series for selected elements from different vegetation types, including those studies by Cole *et al.* (1967) and Ulrich *et al.* (1971), show K most mobile and P with intermediate or low mobility compared with K (Table 6). Depending on vegetation type, Ca and Mg may be intermediate in mobility between K and P. Magnesium and Ca showed lower mobility than P in the Minnesota oak forest and Ca showed lower mobility than P in the Alaskan birch forests.

Differences in turnover rates between chemical elements reflect to a large degree their association in chemical combination and the influence of microbial activity within forest-floor organic matter. Degree of aeration, acidity, and the concentration of associated nutrients such as Fe, P, and Ca may influence mobility of Fe which may exist in different oxidation states or form insoluble complexes with P (Black 1968). The acid nature of birch forest-floor organic matter may be responsible for a lower mobility of Fe and P than in the aspen forest floor. Greater mobility of Mn may reflect the more acid state of birch organic matter. Neutral to slightly basic pH encountered in aspen forest-floor organic matter apparently does not affect reduced mobility of Ca or P in this vegetation type compared with birch. Strongly aerobic conditions which exist in the forest floor in all study areas indicate that much of the Fe probably would be present in oxidized, least mobile forms. Nitrogen, P, and Ca associated in organic combinations in plant and microbial tissues would probably also be conserved and show slower mobilities compared with K, which is not involved in a structural capacity in organic matter. Chelation of cations by various organic matter components may play an important role in nutrient mobility.

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